Proc. Natl. Acad. Sci. USA
Vol. 86, pp. 9876–9880, December 1989
Botany

Dependence of the phototropic response of *Arabidopsis thaliana* on fluence rate and wavelength

(adaptation/blue light/phototropism/fluence response)

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Communicated by Winslow R. Briggs, September 21, 1989 (received for review December 11, 1988)

ABSTRACT **In the phototropic response of *Arabidopsis thaliana* seedlings, the shape of the fluence–response relation depends on fluence rate and wavelength. At low fluence rates, the response to 450-nm light is characterized by a single maximum at about 0.3 μmol·m^{-2}. At higher fluence rates, the response shows two distinct maxima, I and II, at 0.3 and 3.5 μmol·m^{-2}, respectively. The response to 500-nm light shows a single maximum at 2 μmol·m^{-2}, and the response to 510-nm light shows a single maximum at 4.5 μmol·m^{-2}, independent of fluence rate. The response to 490-nm light shows a maximal at 4.5 μmol·m^{-2} and a shoulder at about 0.6 μmol·m^{-2}. Preirradiation with high-fluence 510-nm light from above, immediately followed by unilateral 450-nm light, eliminates maximum II but not maximum I. Preirradiation with high-fluence 450-nm light from above eliminates the response to subsequent unilateral irradiation with either 450-nm or 510-nm light. The recovery of the response following high-fluence 450-nm light is considerably slower than the recovery following high-fluence 510-nm light. Unilateral irradiation with low-fluence 510-nm light followed by 450-nm light results in curvature that is approximately the sum of those produced by either irradiation alone. Based on these results, it is proposed that phototropism in *A. thaliana* seedlings is mediated by at least two blue-light photoreceptor pigments.**

Much of the information about phototropism, as well as its puzzling complexity, is based on measurements of phototropism as a function of the fluence of actinic irradiation. It is generally agreed that the fluence–response relationship for phototropism to single flashes of light consists of a "first positive" response to short light exposures and a "second positive" response to longer light exposures. The first positive response is typically drawn as a symmetrical curve consisting of an ascending arm and a descending arm and covering about 3 orders of magnitude of fluence from 0.01–0.1 to 5–50 μmol·m^{-2} (1–7).

As part of a broad study of phototropism in *Arabidopsis*, we have measured the phototropic response of hypocotyls at a number of fluences and fluence rates. We have found that the shape of the fluence–response curve for short light exposures depends upon the fluence rate and wavelength of the actinic irradiation. Since such a dependence indicates the involvement of multiple blue-light photoreceptor pigments in phototropism, we have tested this hypothesis with a number of dual-wavelength experiments.

The experimental design for the dual-wavelength experiments has been based on a working hypothesis that curvature of a shoot toward light results from differential growth on the lighted (proximal) and shaded (distal) sides of that shoot. The change in growth on each side is considered to arise from some photoproduct produced on that side. Thus, at relatively low fluence levels, this photoproduct is produced on only the proximal side. At higher fluence, the amount of photoproduct on the proximal side will reach some limit, and in addition, photoproduct will be produced on the distal side. Thus, at the higher fluence, the differential amount of photoproduct will decrease, causing a decreased curvature toward light. These aspects will result in a fluence–response relationship with curvature increasing at relatively low fluence, and decreasing at higher fluence to the indifferent region (8). A preirradiation could alter the fluence–response relationship by saturating the amount of photoproduct on one or both sides of the plant, or through a process that has been referred to as adaptation. In adaptation, exposure to a relatively high fluence of blue light at first eliminates the ability to respond phototropically to a subsequent pulse of unilateral light, and the subsequent regeneration of the phototropic capacity is characterized by the fluence–response curve being shifted to higher fluence for some period of time (5, 6, 9).

In this paper, we report that the shape of the phototropism fluence–response curve depends on the fluence rate and wavelength of actinic light. We also report results of dual-wavelength experiments that are consistent with the hypothesis that phototropism is mediated by at least two different blue light-absorbing photoreceptor pigments, other than phytochrome.

MATERIALS AND METHODS

Plant Growth and Irradiation. Seeds of *Arabidopsis thaliana* (L.) Heynh., cv. Estland, were sown and the seedlings grown as described (7), with slight modifications. Strips of microassay wells containing 0.8% (wt/vol) agar supplemented with 1.0 mM KNO_3 were sown with one or two seeds per well. The strips were placed in transparent plastic boxes (21 × 16 × 3 cm), which were sealed with Parafilm and kept for 3 days in darkness at 5 ± 1°C. To potentiate germination, the cold treatment was followed by exposure at 25 ± 1°C to continuous white light for 30 hr (10). At the time of radicle protrusion (i.e., after the 30 hr of white light), the assay rows were moved to and kept in darkness at 25 ± 0.5°C until the end of the experiment.

For phototropic stimulation, the rows of seedlings were removed from the plastic boxes and exposed to unilateral irradiation at 450, 490, 500, and 510 nm, 42 hr after the plants were moved to darkness. In another series of experiments, seedlings were exposed to either 450- or 510-nm light imme-

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diately followed by 510- or 450-nm light, respectively. The seedlings were irradiated at specific fluence rates and for the required durations to give the specified fluences. After the last light treatment, the seedlings were returned to the incubation boxes and kept in darkness for 2 hr ± 5 min at 25 ± 0.5°C and 90% relative humidity. The additional 2 hr was optimal for the development of curvature (7). Gravitropic straightening is insignificant during this 2 hr period. All manipulations were made in complete darkness since green light is not phototropically "safe" (11).

Light Sources. White light for potentiation of germination was provided from white fluorescent tubes at 125 mmol·m^{-2}·s^{-1} (General Electric DeLux). Light for phototropic stimulation was obtained from a slide projector equipped with either a 300-W ELH multi-mirror quartzline bulb in combination with a 3-mm-thick 5% (wt/vol) aqueous cupric sulfate solution or a 250-W halogen-filled tungsten lamp. Wavelength was defined with interference filters with a 10-nm half bandwidth (PTR Optics, Waltham, MA) and peak transmission at 451, 491, 500, or 510 nm. The fluence rate was varied by using neutral density filters and/or by changing the distance between the plants and light source. The fluence rate was measured with an IL 700 A research radiometer (International Light, Newburyport, MA). The duration of actinic irradiation was controlled with a Uniblitz shutter (Vincent Associates, Rochester, NY).

A dual-wavelength irradiation system was used in those experiments in which irradiation was required at two different wavelengths or from two different directions. Two light beams from two different projectors were combined using mirrors such that the seedlings could be irradiated from exactly the same direction with either beam sequentially or simultaneously. Alternatively, one beam could be redirected to irradiate the seedlings from above.

The projector light sources were in one room, and the light beams were directed through a wall into another room, in which the seedlings were irradiated. This use of two separate rooms facilitated exclusion of heat and stray light from the seedlings.

Measurement of Curvature. At the end of each experiment, the seedlings were gently adhered to a sticky transparent tape, keeping the direction of bending in the plane of the tape surface. The tape was then inserted into a photographic enlarger and the images of seedlings were traced. For each exposure in each experiment, a minimum of 60 seedlings were sown. A number of these either did not germinate, were not upright, or were too short to use. Each experiment was repeated 6–12 times, so that each point on the graphs represents the mean value of curvature from 200–400 seedlings.

RESULTS

The fluence–response curves obtained with 450-nm light (Fig. 1*A–D*) were obtained by varying the duration of exposure at each of the fluence rates used. At relatively low fluence rates (0.1 or 0.2 μmol·m^{-2}·s^{-1}), the fluence–response curve for phototropic stimulation (Fig. 1 *A* and *B*) is essentially the same as that previously described for *A. thaliana* seedlings (7), with a single maximum (peak I) at about 0.3 μmol·m^{-2}. However, the shape of the fluence–response relationship becomes more complex at higher fluence rates (Fig. 1 *C* and *D*). At these higher fluence rates (0.4 or 0.7 μmol·m^{-2}·s^{-1}), the response in the so-called "first positive" region of phototropism is characterized by two distinct peaks, peak I, at about 0.3 μmol·m^{-2}, and peak II, at about 3.5 μmol·m^{-2}.

Fluence–response curves were also measured for phototropism at 490, 500, and 510 nm. Fluence–response curves for 500-nm light show a single maximum at about 2 μmol·m^{-2} (Fig. 2*E–H*) for the range of fluence rates used. The fluence–response curve for 490-nm light (Fig. 2*I*) is characterized by a prominent peak at about 4.5 μmol·m^{-2} and a shoulder at 0.6 μmol·m^{-2}. The curve for 510-nm light (Fig. 2*J*) shows a single maximum at 4.5 μmol·m^{-2}.

The dependence of the shape of the fluence–response curves on fluence rate and wavelength (Fig. 1) provides evidence that multiple blue-light photoreceptor pigments are involved in phototropism of *A. thaliana*. Experiments were designed to test this hypothesis and to examine the relationship between these pigments.

To test the possibility that the pigments can be individually saturated, seedlings were sequentially exposed to 450-nm and 510-nm light from the same side. Seedlings irradiated with a unilateral pulse of saturating 510-nm light (25 μmol·m^{-2}, a fluence that, if applied alone, produces curvature at the lowest portion of the descending arm of the fluence–response curve) show a fluence–response curve to 450-nm light with a single peak (Fig. 2*B*). However, seedlings irradiated with a unilateral pulse of nonsaturating 510-nm light (4.5 μmol·m^{-2}, a fluence that, if applied alone, produces a maximum curvature in the fluence–response curve to 510-nm light) show a fluence–response curve to 450-nm light with two maxima (Fig. 2*A*). This curve is essentially no different from the curves obtained without the 510-nm preirradiation (Fig. 1 *C* and *D*). Thus, the unilateral preirradiation with high-fluence (saturation) 510-nm light eliminated the higher-fluence maximum (peak II) in the fluence–response curve to 450-nm light, leaving a curve similar to the one obtained with 450-nm light at low fluence rate (Fig. 1 *A* and *B*). In addition, a preirradiation with unilateral, saturating 510-nm light eliminated the response to a subsequent unilateral 510-nm light pulse (Fig. 2*D*).

In contrast, preirradiation with unilateral 450-nm light at 12 μmol·m^{-2} (0.1 μmol·m^{-2}·s^{-1} for 120 s) eliminated the response to subsequent 510-nm light (Fig. 2*C*). Similar results were obtained (data not shown) with a 450-nm preirradiation at 42 μmol·m^{-2} (0.7 μmol·m^{-2}·s^{-1} for 60 s). These fluences of 450-nm light are in the indifferent region and bring about negligible curvature when applied alone.

To eliminate the possibility that the unilateral preirradiation, itself, induces a curvature, an experiment was designed for preirradiation from above. Preirradiation from above with 450-nm light at low fluence (0.3 μmol·m^{-2}) slightly reduced the response to unilateral 450-nm or 510-nm light, while a similar preirradiation with 450-nm light at high fluence (12 μmol·m^{-2}), eliminated the response to unilateral light of either 450 nm or 510 nm (Table 1). In contrast, preirradiation from above with 510-nm light at either low (4.5 μmol·m^{-2}) or high (25 μmol·m^{-2}) fluence caused no change in the response to unilateral 450-nm light, while the preirradiation with high-fluence 510-nm light eliminated the response to unilateral 510-nm light (Table 1).

To study the interrelationship of the two pigments, the response was measured to a combined irradiation of 450-nm light and 510-nm light, each designed to produce "optimum" curvature. The maximum curvature inducible by a single pulse of 450-nm light of 0.3 μmol·m^{-2} at 0.2 μmol·m^{-2}·s^{-1} is 11.1° (Fig. 1*B*). The maximum curvature inducible by a single pulse of 510-nm light of 4.5 μmol·m^{-2} at 0.4 μmol·m^{-2}·s^{-1} is 10.9° (Fig. 1*J*). Seedlings exposed to unilateral 510-nm light of 4.5 μmol·m^{-2} at 0.4 μmol·m^{-2}·s^{-1}, followed immediately by an exposure to 450-nm light of 0.3 μmol·m^{-2} at 0.2 μmol·m^{-2}·s^{-1}, developed a curvature of 17.9° (Table 2). The curvature was less if the exposure to 450-nm light preceded that to 510-nm light or if the two were given simultaneously.

To distinguish between "saturation" and "adaptation," peak II was decreased by unilateral preirradiation with 510-nm light, and the response to 510-nm light was similarly decreased by preirradiation with 450-nm light. The amplitudes of the maxima were measured as a function of time between the pulses. The results (Fig. 3) show that the

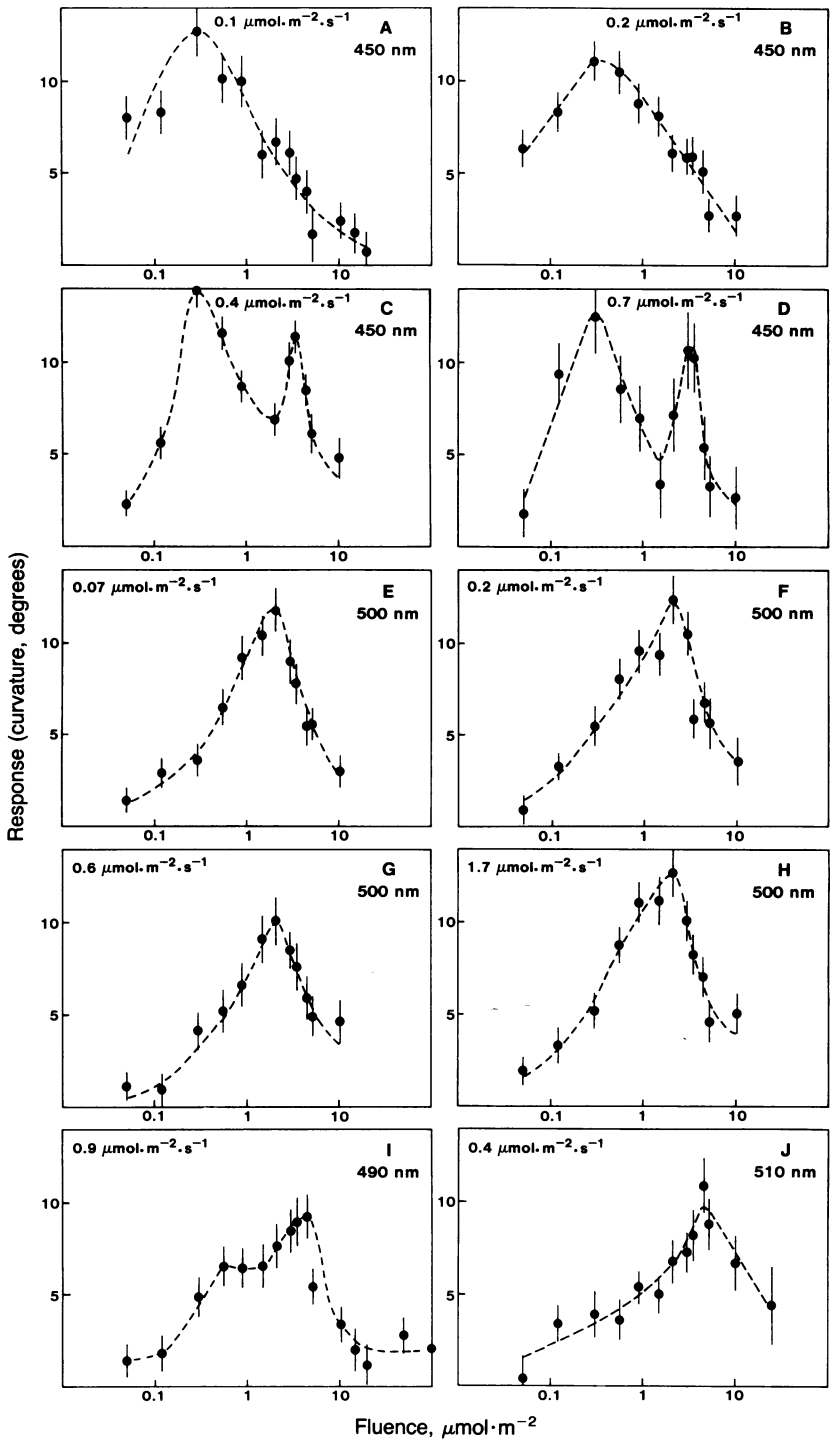

FIG. 1. Fluence–response curves for phototropism by *A. thaliana* to single flashes of light. Individual points represent the mean curvature of 200–400 seedlings. Dashed lines were drawn by inspection. Vertical bars represent ±SEM.

maximum eliminated by an exposure to 510-nm light recovers within 10 min, while the maximum eliminated by an exposure to 450-nm light recovers in 50 min.

DISCUSSION

Two main conclusions may be drawn from the data presented here. These will be stated and supported in sequence.

At Least Two Pigments Are Involved in Phototropism and Contribute to the Complexity of the Fluence–Response Curves. The fluence–response curves that we measured show either one or two maxima, and, for a given wavelength, the shape of the curve may be dependent on the fluence rate. Thus, at least some of these curves are asymmetrical, and, since the shape of the curve depends on the fluence rate, reciprocity is not valid over these fluence rates. A number of factors may have permitted us to see this bimodality and, at the same time, may explain why it was not observed previously (5, 12). In contrast with others, we measured the response of a large number of individual plants at a minimum of 11 fluence values, and we examined the data obtained with each fluence rate separately, not combining them to form one curve. This allowed the bimodality to be observed. This of course assumes that the bimodality is general. Thus far, the bimodality

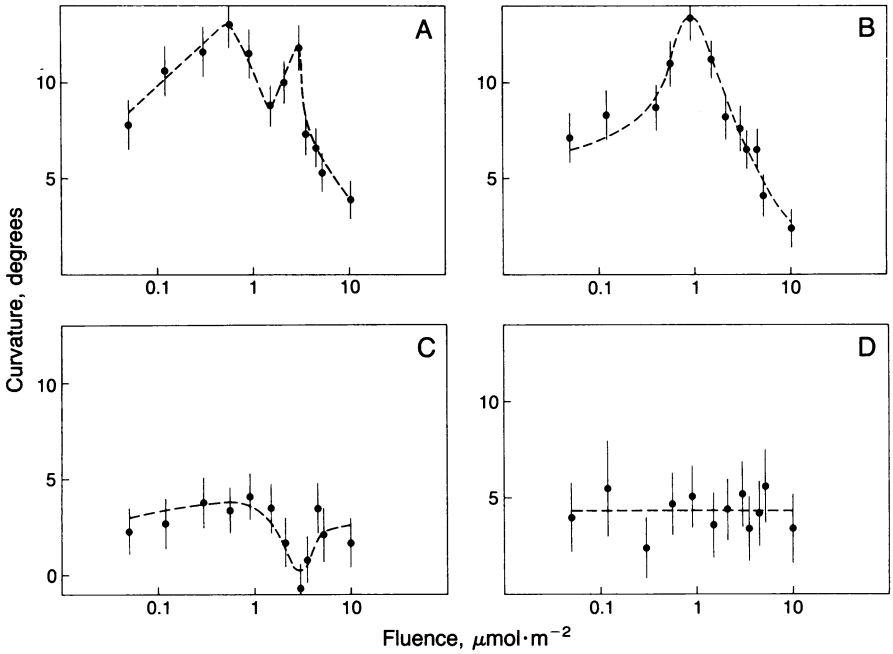

FIG. 2. Fluence–response curves for phototropism by *A. thaliana* to single flashes of unilateral 450-nm or 510-nm light following an irradiation from the same side at 450 nm or 510 nm. (*A*) Preirradiation with 510-nm light (4.5 μmol·m^{-2} at 0.4 μmol·m^{-2}·s^{-1}); response measured to 450-nm light at 0.7 μmol·m^{-2}·s^{-1}. (*B*) Preirradiation with 510-nm light (25 μmol·m^{-2} at 0.4 μmol·m^{-2}·s^{-1}); response measured to 450-nm light at 0.7 μmol·m^{-2}·s^{-1}. (*C*) Preirradiation with 450-nm light (12 μmol·m^{-2} at 0.1 μmol·m^{-2}·s^{-1}); response measured to 510-nm light at 0.4 μmol·m^{-2}·s^{-1}. (*D*) Preirradiation with 510-nm light (25 μmol·m^{-2} at 0.4 μmol m^{-2}·s^{-1}); response measured to 510-nm light at the same fluence rate. Dashed lines were drawn by inspection. Vertical bars represent ± SEM.

has only been observed in two dicots, *Vigna radiata* (13) and now *A. thaliana*.

The dependence of the shape of the fluence–response curve for phototropism on wavelength and fluence rate would not be expected with a single photoreceptor pigment. However, this would be expected if at least two photoreceptor pigments with different absorption spectra were involved in the phototropic response. This conclusion is supported by several additional lines of evidence. First, the higher-fluence maximum (peak II) in the 450-nm fluence–response curve (Fig. 1 *C* and *D*) can be specifically eliminated by a prior exposure to saturating 510-nm light. This 510-nm light can be applied from the side or from above but must be at a fluence expected to produce a response at the low end of the descending arm if administered alone and unilaterally (i.e., a fluence expected to saturate the amount of photoproduct on both sides of the shoot). Such a result would clearly not be expected if the two maxima resulted from the operation of the same pigment.

Second, saturating 510-nm light affects the subsequent response to 510-nm light, while saturating 450-nm light affects the subsequent response to either 450-nm or 510-nm light. The elimination by relatively high-fluence 450-nm light of the response to either 450-nm or 510-nm light (Table 1) and the relatively slow kinetics for the regeneration of responsiveness (Fig. 3) are consistent with the effect that has been referred to as adaptation (9). Based on the data presented here (Table 1; Fig. 3), adaptation is caused by 450-nm light but not by 510-nm light at any of the fluences used.

Third, the fluence–response curve measured for 490-nm light shows a single maximum at 4.5 μmol·m^{-2} and a distinct shoulder at 0.6 μmol·m^{-2}. The least complicated interpretation of these data is that the maximum and shoulder result from two pigments with different dependence on wavelength. Thus, for some wavelengths (e.g., 450 nm), the maxima in the fluence response for the two pigments are sufficiently separated and are resolved as two peaks. For other wavelengths (e.g., 500 nm and 510 nm), the maxima for the two pigments are too close to be resolved. At 490 nm, the resolution is intermediate, and the curve is seen as a single maximum with a shoulder.

Fourth, the two pigments involved in phototropism appear to function independently to a large extent, in that effects of the two wavelengths in producing curvature are additive. Given the phenomenon of adaptation, additivity can be difficult to demonstrate. The cleanest experimental design is an exposure to unilateral 510-nm light followed by an exposure to unilateral 450-nm light. Simultaneous exposure or exposure to the reversed sequence could be complicated by the process of adaptation, which is thought to account for the lower curvature following those treatments (Table 2).

Table 1. Effect of preirradiation from above on phototropic curvature in response to unilateral 450-nm or 510-nm light

Preirradiation	Curvature (mean ± SEM)	
	450 nm	510 nm
450 nm, 0.3 μmol·m^{-2}	7.3 ± 0.9°	6.4 ± 1.0°
450 nm, 12 μmol·m^{-2}	0.7 ± 0.9°	0.2 ± 0.7°
510 nm, 4.5 μmol·m^{-2}	10.6 ± 1.2°	7.5 ± 1.0°
510 nm, 25 μmol·m^{-2}	9.1 ± 1.1°	0.3 ± 1.0°

Fluence for unilateral light, 0.3 μmol·m^{-2} (450 nm) or 4.5 μmol·m^{-2} (510 nm); fluence rate for both preirradiation and unilateral light, 0.1 μmol·m^{-2}·s^{-1} (450 nm) or 0.4 μmol·m^{-2}·s^{-1} (510 nm).

Table 2. Effect of unilateral 450-nm and 510-nm light on phototropic curvature

Irradiation sequence	Curvature (mean ± SEM)
510 nm*	10.9 ± 1.5° (n = 154)
450 nm†	11.1 ± 1.1° (n = 250)
510 nm* followed by 450 nm†	17.9 ± 1.0° (n = 437)
450 nm† followed by 510 nm*	14.0 ± 1.3° (n = 364)
Simultaneous 450 nm† and 510 nm*	14.9 ± 1.0° (n = 457)

*Fluence, 4.5 μmol·m^{-2}; rate, 0.4 μmol·m^{-2}·s^{-1}.
†Fluence, 0.3 μmol·m^{-2}; rate, 0.2 μmol·m^{-2}·s^{-1}.

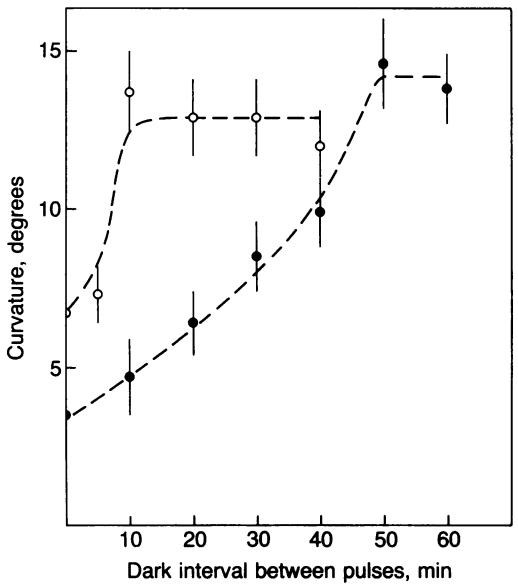

FIG. 3. Kinetics for the recovery of curvature following unilateral preirradiation with 450-nm or 510-nm light. Open circles: plants were irradiated from the side with 510-nm light (25 μmol·m^{-2} at 0.4 μmol·m^{-2}·s^{-1}); after the indicated interval in darkness, the plants were irradiated from the same side with 450-nm light (3.5 μmol m^{-2} at 0.7 μmol·m^{-2}·s^{-1}) and curvature was measured after development in darkness for 2 hr. Filled circles: plants were irradiated from the side with 450-nm light (12 μmol·m^{-2} at 0.1 μmol·m^{-2}·s^{-1}); after the indicated interval in darkness, the plants were irradiated from the same side with 510-nm light (4.5 μmol·m^{-2} at 0.4 μmol·m^{-2}·s^{-1}) and curvature was measured after development in darkness for 2 hr. Dashed lines were drawn by inspection. Vertical bars represent ±SEM.

The Two Photoreceptor Pigments Function Independently. One can conceive of several arrangements of two pigments in phototropism. If either of the pigments transferred its energy to the other, one would not expect an additive response to 450 nm and 510 nm. Additivity of the response indicates that neither is a "trap" for the other, and that any confluence between their actions must be downstream of the limiting step causing the descending arm in the fluence–response relationship. One possible model with which these data are consistent (Fig. 4) contains two separate pigments, P_I and P_{II}. Based on the fluence at which the two maxima are located at different wavelengths, one pigment (P_{II}) absorbs most efficiently at about 500 nm, whereas the other pigment (P_I) absorbs most efficiently at about 450 nm. The saturation of the response that leads to the descending arm and indifferent region in the phototropic fluence–response curve occurs independently for the two pigments. At some point downstream of those steps causing saturation, the two chains converge and pass through another step, which is responsible for adaptation. For the sake of simplicity, this step is presented as an amplifier. The photoreceptor pigment regulating adaptation may be P_I but could be another pigment absorbing well at 450 nm.

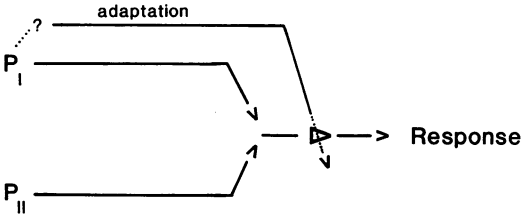

FIG. 4. A possible scheme for the participation of two separate pigments in phototropism. P_I and P_{II} represent the pigments responsible for peak I and peak II in the 450-nm fluence–response relationship. Adaptation is represented as a change in amplification regulated by 450-nm light.

Many other biological responses are known in which multiple pigments participate. Perhaps the classical instance of this is photosynthesis in plants, in which a number of pigments function as "antennae" and "traps" in both photosystem I and photosystem II. In addition, in the sensory system regulating phototaxis in *Halobacterium halobium*, several separate photoreceptor pigments are involved (14). Finally, Galland and Lipson (15–17) have presented compelling data indicating multiple photoreceptor pigments for phototropism in the fungus *Phycomyces*. Although one would not necessarily expect *Phycomyces* and a dicot such as *A. thaliana* to have identical mechanisms for phototropism, our data indicate that *Arabidopsis* may have a photoreceptor pigment system equally as complex as that of *Phycomyces*. As early as 1963, it was suggested that separate systems may function in plant phototropism (2, 3) and contribute to the complexity of the fluence–response curves. It has been shown (18) that mesocotyl curvature in corn is phytochrome-mediated, although this has no dramatic effect on the fluence–response curve for phototropism. The data presented here indicate that multiple photoreceptor pigments contribute to the complexity of the fluence–response curves for phototropism.

The ultimate dissection and measurement of the true action spectrum of each of the photoreceptor pigments for phototropism in *A. thaliana* must await mutants lacking one or more of the pigments. In parallel with this approach, other plants (monocots and dicots) should be tested to see whether they also show these complex fluence–response curves. In addition, the fluence and wavelength dependence of adaptation should be measured.

We are grateful for helpful discussions with Thérèse Best, Bertha Bullen, Norman Good, Rainer Hertel, and Jitendra Khurana. This work was supported by the U.S. Department of Energy under contract DE-AC02-76ER01338.

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